TORSION OF THE CRUSTACEAN LIMB.

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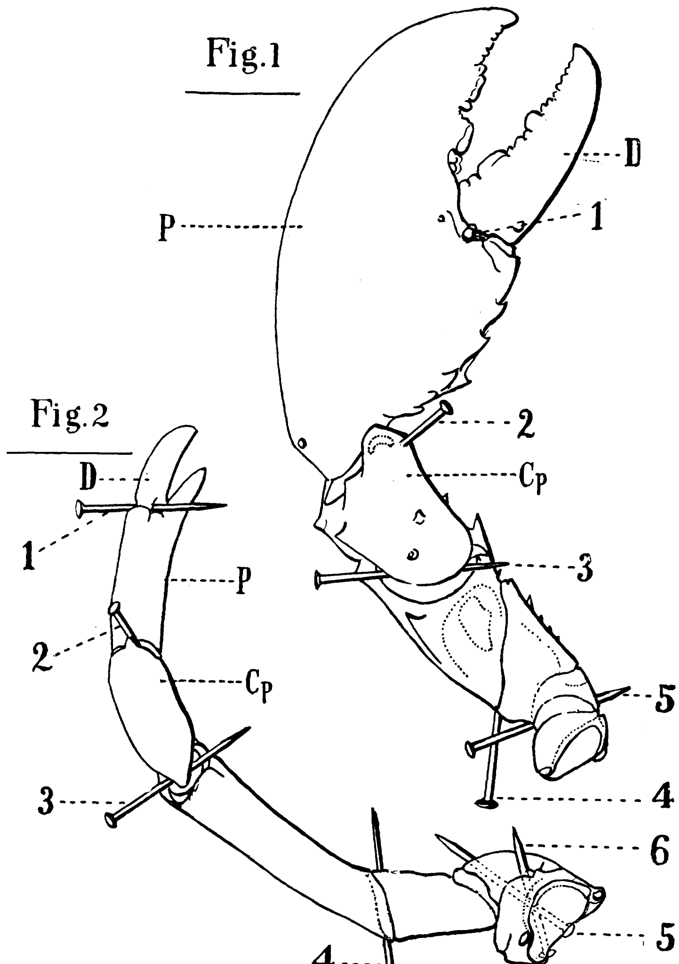
The large double claws or chelæ, which are so conspicuous in many of the higher crustacea, have not failed to attract the attention of naturalists, both on account of their remarkable regenerative phenomena as well as for the aid which they afford to systematic zoölogy. It is therefore the more surprising that attention has never been called to a striking instance of torsion in the great chelipeds of two of the best known forms — the crayfish and the lobster.

If we examine the appendages of either animal from above (Figs. 1 and 2) it will be seen that while in the great claws the dactyles face and open inwards and therefore in a nearly horizontal plane, all the smaller chelæ open upward and outward in a plane which is nearly vertical. In the lobster, however, at the time of birth (Fig. 4) the three pairs of chelate legs, great and small, all have the same form and position, that is, the claws, which are laterally compressed, all open vertically with an inclination outward. It therefore follows that the position of the great 'forceps' has been reversed by rotation through 90°, in consequence of which their inner or anterior faces have become their under sides (Fig 3). The metamorphosis has been reduced to such a degree in the crayfishes that the young are hatched with the essential characteristics of the adult form. If therefore a torsion really occurs in the limbs of these animals, it must be sought in the egg.

In the true crabs, or such representative forms as *Callinectes* and *Carcinas*, the claws open outward, as in the larval lobster, and the outer or posterior face, corresponding to the upper side of the chela of an adult crayfish, tends to become the under side, and is deficient in pigment.

In the crayfish again, about one quarter of the weight of the animal is represented by the great chelipeds, while their proportional weight in the lobster is one half. The acquisition of

size and strength in these limbs, and in *Homarus* the remarkable differentiation into toothed and crushing forceps of either right



FIGS. 1 and 2. Left first and third chelipeds of *Homarus americanus* in natural position, seen from above. Pins 1–5 are inserted close to the hinge joints of the successive segments in each limb, to illustrate the degree of torsion which the great chelipeds have undergone. Compare the position of the hinge-joints 1 and 2, Fig. 1, with that of the corresponding joints in Fig. 2. *Cp*, Carpodite; *D*, dactyle; *p*, propodite; *1–6*, pins inserted in hinge-joints.

or left sides, has been accompanied by a permanent torsion, which has chiefly affected the carpodite, or fifth joint (as counted

from the base — *c. p.*, Figs. 1 and 2). As I shall later show however, this twisting of the limb is entirely independent of the form or weight of the claw. Meantime the eight slender legs, which follow the larger pair, have remained stationary, and have retained their larval form and position.

In the larval lobster the first pair of chelate limbs are prehensile organs solely, by which the food is seized and transferred to the mouth-parts. Later, when the double claw is fully developed, and is provided with either crushing tubercles, or rows of interlocked tooth-like spines, the prey is usually crushed and torn in pieces before its delivery at the mouth by the smaller claw-feet. The toothed or "quick" claw is primarily used for striking and capturing the prey.

The rotation of the chela, in the lobster, is completed at the fourth molt, which marks the most surprising leap in the whole history of development, for at this time the larval swimming organs are laid aside and as Prentiss * has shown, the antennulary pockets or balancing organs come into play, when, for the first time the miniature lobster swims steadily, and in an upright position. At this crisis new instincts also arise; when the lobsterling swims rapidly at the surface, the great claws are directed forward and held close together, but if its pugnacity is aroused, it assumes the well known attitude of defense displayed by an adult animal.

In dead lobsters or crayfishes the large claws, in response to gravity, lie perfectly flat, but this position cannot be assumed in life unless the muscles of the limb are completely relaxed. In the common-position of wariness and defense, the claws are upraised, and tilted obliquely inwards, so that their tips rest close together on the bottom.

In both *Cambarus* and *Homarus* the disposition of pigment is a more striking index of the rotation of the limb than changes in its form, and even more than in the crab have the under sides or what were once the anterior faces of the claws become differentiated by the absence of color. The mottled green pigments which are so thickly spread over the whole upper surface of these animals are completely lacking on the under sides of the big claws.

* "The Otocyst of Decapod Crustacea: Its Structure, Functions, and Development," *Bull. Mus. Comp. Zoöl.*, Vol. XXXVI., 1901.

The large forceps of either side differs in still other respects from the more primitive type-form preserved in the slender feet. Thus the lower margin of the weaker claw of the small cheliped is incurved, as contrasted with the rotund or convex outlines of the big chelæ, a condition probably determined by the greater muscular development of the latter.

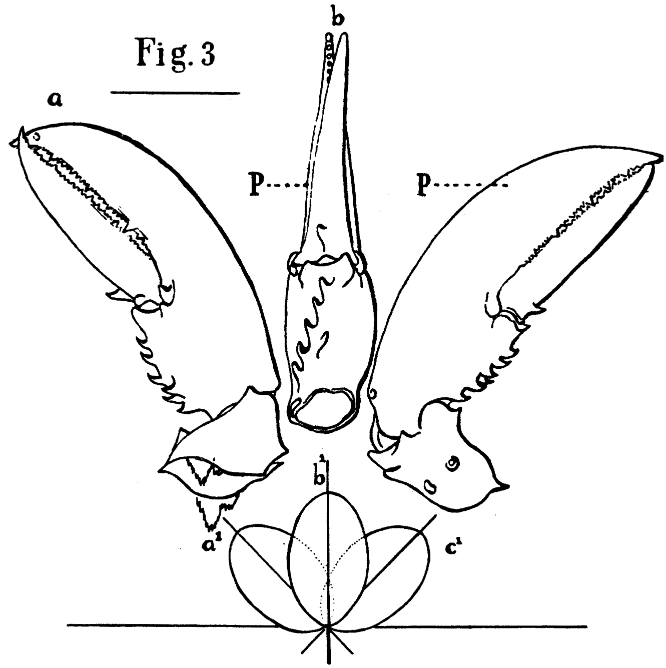


FIG. 3. Illustrating successive positions (a, b, c) in the rotation of the great claws of the lobster, and further by the vertical projection (a^1, b^1, c^1), shown below. In a, a^1, which represents the normal position in the larval lobster and adult crab, the upper or anterior surface of the claw becomes, in the adult lobster the underside c, c^1. P, propodite.

In Figs. 1 and 2, which represent the first and third claw-feet of the left side as seen from above, with the natural foreshortenings, pins are inserted at successive hinge-joints, to illustrate the various degrees of torsion which parts of the limb have undergone. The joints mainly affected are the carpodite and propodite (*Cp*, *P*), and the extent to which they have been twisted may be measured by a comparison of pins (or hinge-joints) marked 1 and 2 in the figures. This phenomenon may

be compared in a general way with the remarkable changes which occur in the metamorphosis of the flat-fishes, where the whole body is more or less completely involved. It seems to be confined to the closely allied Homaridæ (*Homarus*, *Nethrops*), Potamobiidæ (*Cambarus*, *Astacus*) and Parastacidæ (*Parastacus Astacoides*) of Huxley, besides the Paguridæ, or hermit crabs, the Galatheidæ,[1] or Spanish lobsters (*Galathea*, *Munida*), embracing many deep sea forms, which with a number of smaller families are often united into the larger division of the Anomura. In all these forms the dactyles of the large claws appear to open inwards, and although in many cases the smaller feet are non-chelate, or the metamorphosis is abbreviated or at present unknown, we may safely assume that their present state has arisen from a primitive condition such as we find illustrated in the first larval stage of *Homarus*.

That the modification in question was of very ancient origin does not admit of doubt. It was already perfected in the Erymoid crustacea which inhabited the Liassic seas, unless naturalists are wholly wrong in assuming that these primitive macroura were the ancestors of the modern crayfishes and lobsters.

According to Huxley[2] forty species of Eryma have been described from the rocks of the middle Lias up to the Jurassic (Purbeck to Inferior Oolite) formations. In *Eryma modestiformis* of Oppel, the claws open inwards, and the stalked eyes are relatively very large, as in an adolescent lobster.[3] After the death of such an individual as Oppel depicts the large claws would lie flat as in a dead lobster, but had no previous torsion in the limbs of this species taken place, the relaxed claw should have turned the dactyles outward as it does in crabs.

It is interesting to find that in the somewhat less primitive *Eryon arctiformis*, from the Jurassic slates of Solenhofen, a very

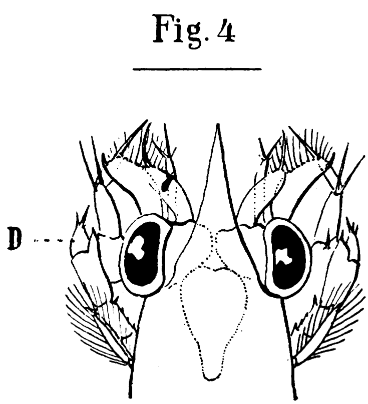
[1] Kinnaman has figured five species of *Galathea*, in all of which, excepting *G. Andrewsii* the large chelæ open inwards, so his drawing is doubtless faulty in this respect. See "A Synopsis of the Britannic Spanish Lobsters and Schrimps," *Proc. Roy. Irish Acad.*, Vol. VIII., Dublin, 1862.

[2] "On the Classification and Distribution of the Crayfishes," *Proc. Zoöl. Soc. London*, 1878, and "An Introduction to the Study of Zoölogy," illustrated by the Crayfish. New York, 1893.

[3] See p. 163 and plate 8, "The American Lobster," Bull. U. S. Fish Commission, Washington, 1895.

decided approach to the brachyurans, or true crabs is seen in the short tail, the broad carapace armed with marginal spines, as well as in the slender antennæ and other appendages so far as they are known. Very significant also is the fact that as in the modern crab the claws open obliquely outward.

In the homarine *Hoploparia*, found in the Cretaceous and early Tertiary periods, the form of the large chelipeds renders it highly probable that a torsion of this limb had already taken place. At all events this phenomenon has a very ancient history, and is probably older than autotomy which precedes the regen-



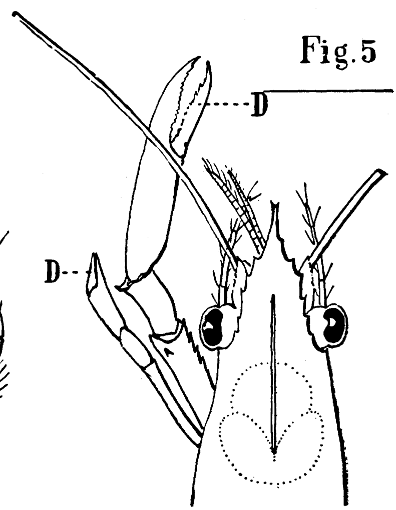


FIG. 4. First larva of lobster from above, showing the outwardly opening claw of the first pair of chelipeds. *D*, dactyle.

FIG. 5. Fourth larva or lobsterling stage of the lobster, showing the big claw-feet, in which torsion is complete, opening inward, toward the middle line of the body. *D*, dactyle.

eration of certain limbs, and which in the most perfect cases is dependent upon a fusion of the second and third joints. In the lobster this fusion does not occur until after the fifth molt.

II.

When we attempt to answer the question — How could a torsion of the crustacean limb be effected? — the results are not very reassuring upon either Lamarckian or Darwinian principles. The

conditions of the problem seem to be very simple, and can at least be stated with a certain degree of exactness.

The segments of the limb mainly affected (Figs. 1 and 2) are the fifth and sixth (*P* and *Cp*, Figs. 1 and 2) which move on hinge joints. Each has a hard tubular shell, and lodges two muscles, a flexor and extensor, the fibers of which originate on the inner surface of the shell, and are inserted on tendons which engage with the next or distal segment, the mobility of the limb being further secured by soft interarticular membranes, and a series of hinge or peg-and-socket joints, set in different planes (Figs. 1 and 2). When the flexor muscle, let us say, of the carpus or fifth joint contracts, the huge claw moves on its hinge and is drawn upward and inward, as a door might be opened by means of cords, worked at a distance: at the same time the fibers react on the inner surface of the tubular shell, but the hinge-joint is fixed, and no conceivable contraction of such fibers can convert a straight pull into a twist. There is no room for the shifting or migration of the muscles, but this would not affect the conditions one way or another. Torsion has not occurred as a result of the normal movements of the limb.

It is to be noticed that the rotation of the claws occurs in larval life before the chelæ attain their full development, but if in the course of the evolution of these forms the increasing weight of the claws could have had any effect upon their ultimate position, it should have turned them in the opposite direction, because they lean outward in the larva. The theory that the effects of strain or use are inherited is therefore incompetent to account for the modification which exists.

In the present case it seems equally impossible to apply the selection theory of Darwin, and it would tax the imaginative faculty to determine wherein the chela of a crayfish was better adapted for prehensile purposes than the claws of hundreds of prawns, or how the toothed claw of the lobster excelled in this respect the pincers of the blue crab, *Callinectes*, or as a weapon of offence, the slashing, sabre-like, out-turned dactyles of *Alpheus heterochelis*, and of many another species of this large genus. I refer only to the power and ease of seizing, and not to the muscular force or to the armature of the claws itself, which is another

question. But the height of the difficulty is not yet reached, for upon the selection theory, the torsion of such limbs must have arisen gradually, through successive fractions of a degree, until the member had moved through a quadrant of arc ; furthermore we are required to believe that each successive position was so much more favorable than the last, that forms showing such as well as possibly other correlated variations would outstrip their competitors, and alone leave descendents. As already suggested, the problem is somewhat analogous to the migration of the eye in the metamorphosis of flat-fishes, attempts to explain which in terms of the selection theory have not been very successful.

The difficulty of the problem is not lessened when we reflect that the slaughter of the young in a form like the lobster, takes place on a tremendous scale and is of the most indiscriminate character, before the prehensile organs are fully developed. We can only *guess* at the causes of such a variation. Its great antiquity, dating from as early at least as the Jurassic period, and other considerations already touched upon, render it highly probable that it first arose as a discontinuous variation. That it was not indispensable, is suggested by its erratic distribution at the present day.

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